Should I stay or should I go? Host plant quality mediated trade-offs in the forest tent caterpillar

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ABSTRACT

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Christopher Plenzich

Group living has both negative and positive effects, and various ecological factors can mediate decisions between remaining cohesive and splitting up. We investigated how food quality mediates the trade-off in *Malacasoma disstria*, the forest tent caterpillar, between (i) remaining in a group on a known food source, thus benefitting from group basking and group predator defenses, but potentially incurring opportunity costs, and (ii) increasing movement in search of a potentially better quality food source and/or splitting into more numerous groups, risking predation. During laboratory experiments in spring 2013, and field experiments in 2014, groups of caterpillars were reared on the foliage of two different tree species; one of high quality: trembling aspen (*Populus tremuloides)*, and the other of lower quality: sugar maple (*Acer saccharum)*. Results indicate that forest tent caterpillar colonies feeding from maple increased locomotion, traveled farther, took more numerous, but smaller meals, and split into smaller, more numerous groups when compared to colonies feeding from aspen. Though other ecological factors were found to mediate group decisions, namely developmental stage, colony size, and wind speed, the presented experiments suggest that a decision between remaining cohesive or otherwise in the presence of different quality food sources exists. The findings suggest that the potential increase of encountering a predator when increasing movement and decreasing cohesion can increase early larval mortality and may be a contributing factor to the rise and decline of an outbreaking population.

Acknowledgements

Three years ago, I was a wide-eyed student, ready to take on a master's project. Little did I know that this very project would take over my life (in the best way possible, of course). After a myriad of conference presentations, collaborating on an international art exhibit, winning a few competitions, and a couple of panic attacks, this adventure has come to a bittersweet end.

I would first like to thank Dr. Emma Despland for accepting me into her lab and allowing me to do more work with caterpillars than I ever imagined possible. Thanks lab mates Jessica Ethier, Michael Gasse, Emilie Dion, Solène Sagne, Gaspar Legendre, volunteers Jackie Peters, Lisa Walker, JP Maillet, Chris Daignault, Katherine Levasseur, and committee members, Dr. Ferguson and Dr. Fraser. Thanks to Ministry of Natural Resources and Forestry of Ontario staff for supplying egg masses and the Morgan Arboretum staff for allowing me to conduct research at the arboretum.

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-This is for the caterpillars; the true stars of this project-

"In the cosmic view, the caterpillar is more than an insect, more than a fragment of life. The tent caterpillar is the universe. One cannot ask the purpose of the tent caterpillar. One can only observe it and marvel."

- Vincent G. Dethier, *The world of the tent makers* (1980)

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1. Introduction

Murders, clouds, memories, or pods: many different animals live in groups (see Beauchamp, 2014 and references therein). Group living implies that multiple organisms of the same species, and sometimes of different, must make collective decisions to remain cohesive. Individual behaviors, preferences, and requirements nevertheless vary, thus the group must reach some form of collective consensus that balances these needs. Group consensus is most often partially shared between group members, but can be completely unshared, where one individual decides for the entire aggregation, or shared, where all members of the group decide together. For example, eusocial insects often partially share decision-making in the form of task allocation; individuals decide based on local necessity without much conflict. Alternatively, in the case of navigating birds, it has been documented that in some cases, more experienced birds make decisions for the group, although if the group is particularly large, such as skylarks (*Alauda arvensis*) or pigeons (*Columba livia*), it becomes more likely that decisions are more readily shared (Conradt and Roper, 2005 and refrences therein).

Group living benefits have been well documented in a wide range of taxa. General advantages of group living tend to be separated into two broad categories; foraging advantages and increased predator avoidance/detection, though these benefits may vary among taxa (Rubenstein, 1978). For example, the former holds true for eusocial insects, such as bees and ants, which use sophisticated communication to recruit colony-mates to favourable food sources (Travers, 1993; Bernstein, 1975). Furthermore, increased predator defences, such as many-eyes hypothesis or dilution and selfish herd effects, have been observed in gregarious mammals (Hass and Valenzuela, 2002), amphibians (DeVito, 2003) and caterpillars (McClure and Despland, 2011). Though not included in the two main groups of general group-living advantages,

thermoregulatory benefits have also been documented; it has been found that some animals, for instance reptiles and caterpillars, reap thermal benefits, such as group basking, when remaining cohesive (Shah et al., 2003; McClure, Cannell, and Despland, 2011).

Conversely, disadvantages of remaining cohesive exist, including: an increase in resource competition, leading to less nutrient intake per individual; an increased potential to transmit disease, pathogens, or parasites from one individual to another; an increase in the potential for aggression within the group; and a possible increase in being detected by predators (Rubenstein, 1978). Similar drawbacks have been exhibited by carnivores (Gittleman, 1989) social insects (Costa and Ross, 1993) and even sessile invertebrates (Buss, 1981), suggesting that comparable disadvantages of group living may exist among a wide range of gregarious species.

Because both negative and positive effects of group living exist, research has been conducted into how various ecological factors mediate decisions in terms of either remaining cohesive, separating into smaller, more numerous groups, or abandoning cohesion all together. One comprehensive review (Elgar, 1989) of studies regarding predator vigilance and group size in mammals and birds found that, in general, individuals in larger groups spent less time being vigilant and more time foraging (many-eyes hypothesis), hence benefitting more from grouping. However, other factors were found to constrain group size, one of the most widely studied being food density, where, generally, aggregations split into smaller groups in areas of lower food density (Elgar, 1989; Beauchamp, 2009). It is argued that food quality may also be an important factor which mediates decisions between remaining cohesive or otherwise, however, the resulting effects on group size or group splintering have not been widely studied (Elgar, 1989; see also Elgar, 1986). In a more recent review of studies examining the effects of food density on the relationship between group size and predator vigilance, the authors found that only one of the

studies incorporated the effect of food quality (Beauchamp, 2009 and references therein). A study (Nystrand, 2007) conducted on a social bird species, the Siberian jay (*Perisoreus infaustus*), found that the birds exhibited conservative foraging strategies; the birds generally spent more time feeding on higher quality food when predators were absent, but remained on lower-quality food sources when predators were visible in the areas of higher quality food, indicating a trade-off between safety from predators and food quality. Forest tent caterpillars also exhibit conservative foraging decisions with the use of pheromone trails (McClure and Despland, 2011). In one study, the caterpillars were more likely to remain on a known food source, irrespective of food quality, when marked trails were absent to the higher quality food source, but relocated to a higher quality food source when pheromone trails were present. The findings suggest that forest tent caterpillars, though not displaying signs of vigilance, use pheromone trails to reduce unknown exploration costs (Santana et al., 2015), where marked trails represent a safer route when compared to non-marked territory (McClure, Ralph, and Despland, 2011). Other behavioral compromises have been documented with the ant species *Lasius pallitarsi*. Researchers found a trade-off in foraging strategies where in the presence of predators at a high quality food patch, the risky high quality patch was used just as often as a no-risk lower quality food patch as long as the potential for growth was larger than the potential of encountering a predator. Similar compromises have been documented in other ant and shoaling fish species (Nonacs and Dill, 1990 and references therein). The presented examples demonstrate how food quality can be an influential factor in group foraging decisions, however they do not provide predictions in terms of how food quality affects group size or group splintering, though it is believed that smaller groups may form in areas where lower quality food is present (Elgar, 1989; see also Elgar, 1986).

Because comparable effects of food quality on foraging decisions have been reported among the studied species, though the direct effects on grouping are unknown, I propose using the forest tent caterpillar, *Malacosoma disstria* Hübner (Lepidoptera: Lasiocampidae), as a model to research how food quality mediates decisions between remaining cohesive or splitting into smaller groups.

Social caterpillars are argued to be good models to determine whether decisions increase fitness as the following characteristics have been documented among a range of species: (i) the effects of food intake on growth or reproduction must be known (ii) populations must be susceptible to measurable predation rates (iii) colony foraging decisions must affect their level of predation risk (Nonacs and Dill, 1990). The forest tent caterpillar fulfills these requirements.

Of the whole genus, the forest tent caterpillar is the only known nomadic forager, and unlike others in the same genus, it does not construct tents. Instead, the forest tent caterpillar builds silk mats, known as bivouacs, which are regularly abandoned by the group when foraging (Fitzgerald and Costa 1986). After a typical 5 moults, each stadium lasting approximately 1 week, caterpillars pupate individually. Adults with non-functional mouths emerge weeks later and within a few days, mate, oviposit (females), and die (Fitzgerald 1995).

Mating takes place in mid-summer and eggs overwinter in masses as bands around host tree twigs. Synchroneity between hatching and bud-break is crucial for proper development; caterpillars hatch in early spring, as leaves are budding, which in turn allows caterpillars to maximize larval growth rate by feeding on nutrient-rich young leaves (Hunter and Lechowicz, 1992). As caterpillars grow and forage, pheromone-laced silk trails are produced by individuals, mapping trails to known food sources and enabling the colony to remain cohesive. Individuals differ in exploratory behavior where active individuals are more likely to explore unmarked

territory, while others remain more quiescent and travel only in the presence of pheromone trails (Nemiroff and Despland, 2007). At early developmental stages, or instars, caterpillars exhibit high cohesion, but display more independence later in their life-cycle, likely in order to decrease potential resource competition (Fitzgerald 1995). *M. disstria* is considered to be one of the most important defoliators of deciduous trees across North America and can be easily spotted in outbreaking years (Fitzgerald 1995), feeding on a range of food sources which can differ from locale to locale (Parry and Goyer, 2004).

Group living is key for survival for forest tent caterpillar colonies (Despland and Le Huu, 2007). Caterpillars benefit from collective thermoregulation (McClure, Cannell, and Despland, 2011), and collective anti-predator defenses, including somewhat passive defense strategies, such as selfish-herd effects and predator saturation, especially at early instars, and more active defenses such as head-flicking or thrashing, where defenses vary according to predator (McClure and Despland, 2011).

Pheromone-laced silk trails direct group movement (Fitzgerald and Costa 1986); however, due to pheromone trail adherence, it is possible for caterpillars to become trapped on lower quality food sources (Dussutour et al., 2007). This may lead to a delay in development as a minimal larval weight is required for pupation to occur (Etilé and Despland, 2008). Nutrient deprivation from being trapped on a low quality food source for an extended period of time (due to trail adherence) has been demonstrated to increase exploratory behavior in individuals, leading to an increased probability of discovering a novel food source. Therefore, as individuals become more nutrient deprived, they have a higher tendency to leave a marked trail and initiate exploration (McClure et al., 2013); this increased movement can potentially increase predation (McClure and Despland, 2010).

M. disstria from Quebec, Canada have demonstrated a preference for trembling aspen, *Populus tremuloides* (hereinafter aspen), over sugar maple, *Acer saccharum* (hereinafter maple) (Levesque et al., 2002; Etilé, 2008). Furthermore, this caterpillar species exhibits poorer development while feeding on maple when compared to aspen (Lorenzetti, 1993) which may be due to less soluble sugars (Panzuto et al., 2001) and more tannins present in the former (Lorenzetti 1993). It can therefore be considered that for the forest tent caterpillar, maple is a lower quality food source when compared to aspen.

In general, this research aims to study the differences in collective foraging behaviors of the forest tent caterpillar, especially at early developmental stages, between colonies feeding on maple and aspen. In particular, this research aims to investigate how food quality mediates trade-offs between (i) remaining in one large group on a known food source, thus allowing the individuals to reap the maximal benefits of group living, but potentially incurring opportunity costs, and (ii) increasing movement in search of a potentially better quality food source and/or decreasing the level of cohesion (i.e. splitting into more numerous groups within the colony), leading to a potential increase in predation.

Two research experiments have been conducted to study such potential trade-offs, working complementary to one another. The first experiment, conducted in a laboratory setting, offers great resolution for behavioral observations, however, caterpillars were inevitably confined to small areas. The second experiment, where caterpillars were observed *in situ*, does not offer as great resolution for behavioral observations, however caterpillars were not confined to small areas, allowing for measurement of natural movement.

As forest tent caterpillars have been shown to initiate exploration when protein-deprived (Colasurdo et al., 2007), predictions of caterpillar behavior when fed a lower quality food source

(maple), compared to that of a higher quality food source (aspen), include (i) less cohesion, (ii) more time spent in locomotion, (iii) travelled farther. Furthermore, larvae reared on maple are expected to attain lower mass than those reared on aspen (difference in performance; see Lorenzetti 1993), and are expected to take many small meals rather than a few large ones, leading to a higher number of meal initiation points (difference in preference; see Levesque et al., 2002; Etilé, 2008).

2. Methods and materials

2.1. Behavioral observations

Similar behaviors were used as the basis for observations in both the laboratory and field experiments, namely colony activity and cohesion. Activity was defined simply as locomotion or not, since it was difficult to differentiate between feeding and quiescent caterpillars. A colony was considered to be engaged in locomotion if the majority (over 50%) of the individuals were walking; that is, moving forward. Because caterpillars feeding on maple were predicted to be less synchronous than those feeding on aspen, a threshold of 50% was chosen to avoid missing colony activity in the case of highly asynchronous behavior. For similar reasons (in case of asynchronous behavior), cohesion was represented by the number of groups, with a group defined as at least 5 caterpillars all within 1 body length from each other, and more than one body length away from another group (see Despland and Le Huu, 2007; Allen, 2010; McClure and Despland, 2011; for group size where a group of 5 caterpillars suggest individuals reap at least some benefits of group living).

2.2. Laboratory experiment – Larval rearing and set-up

Egg masses were obtained from the Kenora (49°46′N 94°29′W) and Dryden (49°47′N 92°50′W) districts of western Ontario from aspen trees (figure 1). While not in use, egg masses were refrigerated at 4^{o}C. The first egg masses were removed from refrigeration when local bud break of maple and aspen trees was observed (approximately 07-May-2013).

Maple and aspen leaves used for rearing were collected haphazardly from Bois-De-Liesse (45°30′20″N 73°45′50″W) and Complex Environmental St. Michel (45°33′48″N 73°37′44″W)

(figure 1). Multiple large branches from each tree species were collected and kept in water for a maximum of 3 days. The smallest, newest leaves were used during rearing and video recording.

Egg masses and leaves were cleaned prior to rearing to help inhibit the spread of the nuclear polyhydrosis virus (NPV) (Grisdale, 1985). NPV is a virus which commonly infects insects, notably moth and butterfly larvae, causing sluggish behavior in the host, and eventually death (Stairs, 1965). Egg masses were bathed in a 6% sodium hypochlorite solution for 1.5 minutes, then rinsed in water for 5 minutes. Finally, the egg masses were submerged in a 0.06% sodium hypochlorite solution, completing the cleaning process. Leaves to be used for rearing were bathed in a 0.06% sodium hypochlorite solution for approximately 30 seconds and left to air dry (Grisdale, 1985). Unused egg masses remained refrigerated. Caterpillars originating from the same egg masses can be considered siblings (Fitzgerald and Costa, 1999) and will hereafter be referred to as one "colony".

When not being recorded, caterpillar colonies were reared in separate sealable, reusable 1.22 L plastic containers with a mesh screen embedded into the lid, and later relocated to larger, 4 L plastic containers once the colony reached the third instar (L3) and outgrew the smaller container. The containers were placed under a UV light for approximately 5 minutes on each side prior to housing the caterpillars, to help prevent the spread of NPV. Each container contained a dampened paper towel and wax paper placed on top, fitted to the bottom of the container. Caterpillars received a 16 hour light and 8 hour dark photoperiod with 70% relative humidity at 21^{o}C. Caterpillars were fed *ad libitum* with either maple or aspen, according to their treatment group (Addy, 1969). Recording began 07-May-2013, and ended 29-May-2013.

Caterpillars were observed at the hatchlings (L1), second instar (L2) and fourth instar (L4) stages, since forest tent caterpillars are most cohesive at early developmental stages

(Fitzgerald 1995). Caterpillar colonies were filmed in separate 9 mm petri dishes. Each petri dish contained the following: a dampened paper towel cut to the size of the petri dish, a same-sized disc of wax paper placed on the wet paper towel, and one leaf (maple or aspen) affixed to the wax paper with a reusable adhesive (sticky tack). The petiole of the leaf was placed in a closed microfuge tube filled with water.

For hatchling observations, an egg mass was placed in each dish and filmed. Observation began with the first individual coming into contact with the food source. After filming, the colonies were transferred to fresh rearing containers.

For L2s and L4s, approximately 20 haphazardly chosen individuals per colony were taken out of incubation, placed together in their respective petri dishes with their respective leaf species and filmed. Scoring began 2 hours after the caterpillars were placed into the petri dish to allow them to acclimate. Individuals were returned to incubation with the rest of their respective colonies once filming was completed. Caterpillars which hatched while in storage were grouped together to form a new colony as forest tent caterpillars do not discriminate kin from non-kin (Fitzgerald 1995). These colonies, referred to as “orphan colonies”, were filmed at the L2 and L4 stages when possible.

A maximum of 6 different dishes were filmed at a time, in a covered box with fluorescent lighting. Each filming bout began at approximately noon and took place for 18 - 24 hours. To standardize observation time, only 8 hours of video were used for behavioral observations per colony per instar. Noldus Oberver XT version 5 was used for the behavioral observations. Meal initiation points, the points in which a colony begins feeding on the leaf, were counted as they appeared.

2.3. Laboratory experiment – Statistical analysis

For aspen-reared colonies, 14 L1, 15 L2, and 8 L4 colonies were used for behavioral observations. For maple-reared colonies, 15 L1, and 6 L2 colonies were scored. Fewer maple-reared colonies moulted to L2 due to heavy mortality as maple-reared colonies ceased feeding; no maple colonies moulted past the second instar. Furthermore, high mortality due to NPV was experienced at the third and fourth instar for the aspen-reared colonies, leading to the death of all but 9 fourth instar colonies; 1 sole colony pupated, though colonies which were believed to infected were not used for behavioral observations (table 1).

Videos which were not used for analysis were either too distorted to properly observe behaviors or those in which colonies did not reach the food source (table 1).

Percent time spent walking and percent time spent in one group was obtained from the preliminary statistic output of The Observer XT. As the data were presented as a proportion, (percent time spent per behavioral observation) data were transformed using the logit transformation (Warton and Hui, 2011). The following formula was used where 'p' is the proportion in question:

$$logit(p) = \log\left(\frac{p}{1-p}\right)$$

Two-way factorial ANOVAs were performed for both the locomotion and cohesion transformed data sets using the food source, either maple of aspen, and instar, either L1 or L2, as independent variables. One-way ANOVAs were performed for the locomotion and cohesion transformed data sets to test for differences between the L1, L2, and L4 aspen-reared colonies. All transformed data were tested for homoscedasticity using Levene's test and verified graphically using a quantile-quantile plot. In all cases, the data did not differ significantly from normality nor homoscedasticity.

A zero-truncated poisson regression was used for analysis of the meal initiation points using the instar and food source as possible explanatory variables. Similar results were obtained for both forward and backward step-wise models of the zero-truncated poisson regression, and the sign of the beta coefficient, β, dictates the type of relationship, either negative or positive, between the meal initiation points and the explanatory variables.

All data were analyzed using R version 3.1.1 at the 0.05 significance level.

2.4. Field experiment – Larval rearing and set-up

In 2014, egg masses were once again obtained from the Kenora and Dryden districts of western Ontario from aspen trees (figure 1). While not in use, egg masses were refrigerated at 4ºC. Caterpillars were reared on maple and aspen trees at the Morgan arboretum (45°25′50.1″N, 73°57′8.2″W), and observed in-situ (figure 1). Egg masses were not cleaned prior to research.

To ensure synchronization between hatching and bud-break, egg masses were haphazardly affixed to either aspen or maple tree branches less than 2 m above ground level with the use of plastic zip-ties on three separate days; 2-May-2014, 6-May-2014, and 8-May-2014. Each colony was identified using a bright tape tied closely to the egg mass with an alphanumeric code specific to the colony.

Observations were made at 1 hour intervals during daylight for approximately 8 hours per day between 9h00 and 18h00; past experiments suggested that caterpillars are most active between 7h00 to 21h00 (McClure and Despland, 2010). Colony activity (locomotion), cohesion, and exposure to sunlight were recorded at each observation. Hourly temperature, wind speeds, humidity levels, and atmospheric pressure were recorded using archived data from the Environment Canada website from the St. Anne-De-Bellevue weather station, located at the

entrance of the Morgan Arboretum. The number of individuals per colony were counted after the last observation of the day. Observations were conducted by hand on prepared sheets with the help of an assistant and later transcribed digitally. Observations were not conducted on rainy days as past experiments demonstrated that the caterpillars would not be active (McClure and Despland, 2010).

Between 14 and 18 colonies per tree species were observed daily. Colonies hatched on different days, and observed colonies occasionally travelled too far for observation or died, which accounts for the discrepancy in number of colonies observed per day. Observations were recorded for a total of 6 days between 12-May-2014 and 21-May 2014, totalling 1457 individual observations (an average of 16 colonies per tree species, 8 hourly observations per day, for 6 days). Additional colonies were placed on each tree species to record mortality rates; 3 on aspen and 20 on maple.

On 15-May-2014, 20-May 2014, and 25-May, 2014, colony dispersal was recorded: the distance between the colony and the closest abandoned bivouac and the distance between the colony and its egg mass were measured using a soft measuring tape along the tree, following the shortest possible distance along the tree branches between the colony and the bivouac or egg mass. In addition, on 29-May-2014, 30-May-2014, and 01-June-2014, several individuals per colony at L4 were selected haphazardly and weighed, totalling 76 caterpillars. Colonies were removed from the trees at the moult to the fourth instar, when colonies began travelling too far up the trees and were no longer easily observable.

2.5. Field experiment – Statistical analysis

At the beginning of the experiment, maple and aspen-reared colonies were similar in size with maple-reared colonies having an average of (mean±95% CI) 108.0±21.3 individuals per colony (n=37) and aspen-reared colonies having an average of 110.4±32.6 individuals per colony (n=17). Similar to the laboratory experiment, higher mortality was experienced when rearing caterpillars on maple than on aspen. A t-test was performed to determine if the difference in caterpillar survival was significant between maple and aspen-fed colonies.

Mixed effects logistic (binomial) regressions were used to determine which factors caused the caterpillar colonies to separate into multiple groups (together in one group vs not in one group) and which factors caused the caterpillars to engage in locomotion (walking vs not walking). A zero-truncated poisson regression using the number of groups per colony was performed to determine if different variables from the cohesion logistic regression contributed to the colony splitting into more numerous groups. The following variables were used as possible explanatory variables for the regressions: food source, days post hatch (as a proxy for developmental stage), time of day (categorically, by hour), temperature, atmospheric pressure, wind speed, humidity, colony size, and sunlight exposure (in direct sunlight or not). In the case of the mixed effects logistic regressions, the colony nested within the respective food source treatment, either aspen or maple, was used as the random effect. In all cases of regressions, similar results were obtained for both forward and backward step-wise models. The sign of the beta coefficient, β, dictates the type of relationship, either negative or positive, between the independent variable and the explanatory variables.

A two-way factorial ANOVA was used for the measured distances between the colony and its egg mass taken on the three separate days. Additionally, random block ANOVAs were to

compare caterpillar mass and distance between the colony and the closest abandoned bivouac between the two different tree species on the days these measurements were taken.

Normality for all continuous variables were tested for homoscedasticity using Levene's test and verified graphically for normality using a quantile-quantile plot. Only caterpillar mass and caterpillar survivorship was found to not differ significantly from normality. Non-normal data were transformed using the logarithmic transformation, re-tested, and were not found to differ significantly from normality nor homoscedasticity.

All data were analyzed using R version 3.1.1 at the 0.05 significance level.

3. Results

3.1. Lab experiment

3.1.1. Cohesion

Aspen-reared colonies spent a larger percentage of time in one group than maple reared-colonies ($F_{[1,45]}$=32.1, p<0.001, figure 2) and first instar caterpillars spent a larger percentage of time in one group than second instar caterpillars ($F_{[1,45]}$=10.4, p=0.002, figure 2). No significant interaction between instar and tree food source was found ($F_{[1,45]}$=0.553, p=0.461).

A significant difference in percentage of time spent in one group was found when comparing the first, second, and fourth instars of aspen-reared colonies ($F_{[2,34]}$=13.7, p<0.001). A Tukey HSD post-hoc test revealed that fourth instar aspen-reared colonies spent less time in one group that first instar aspen-reared colonies (p<0.001, figure3), and second instar aspen-reared colonies (p=0.0053, figure 3), however, first and second instar aspen-reared colonies spent a similar percentage of time in one group (p=0.072, figure 3).

3.1.2. Locomotion

Maple-reared colonies spent a larger percentage of time engaged in locomotion than aspen-reared colonies ($F_{[1,45]}$=39.4, p<0.001, figure 4). No significant different in percentage of time spent walking was found between first and second instar caterpillars ($F_{[1,45]}$=2.59, p=0.114, figure 4), however a significant interaction between instar and food source was found ($F_{[1,45]}$=6.59, p=0.014, figure 4), where second instar maple-reared caterpillars spent less time walking than first instar maple-reared caterpillars.

First, second, and fourth instars of aspen-fed colonies all spent a similar percentage of time engaged in locomotion ($F_{[2,34]}$=0.222, p=0.802, data not shown).

3.1.3. Meal initiation points

Maple-reared colonies took more numerous meals (median=3, n=20) (i.e. more meal initiation points) than aspen-reared colonies (median=1, n=29) (β=1.02, Z=3.49, $p<0.001$).

In regards to the first, second, and fourth instars of aspen-fed colonies, only first instar caterpillars took fewer meals (median=1, n=14) (i.e. less meal initiation points) compared to fourth instar caterpillars (median=2.5, n=8) (β=-1.2407, Z=-2.48, p=0.013).

3.2. Field experiment

3.2.1. Cohesion

Maple-reared colonies were less likely to be observed in one group than aspen-reared colonies (β=-1.07, Z=-4.24, $p<0.001$), and larger colonies with more individuals were less likely to be observed in one group (β=-0.0167, Z=-6.91, $p<0.001$). No other predictor variables were found to be significant.

The Poisson regression showed that maple-reared colonies were split up into more numerous groups than aspen-reared colonies (β=0.940, Z=4.88, $p<0.001$). Larger colonies also split into more numerous groups (β=0.00768, Z=15.1, $p<0.001$). Additionally, as wind speed increased, colonies were observed in more numerous groups (β=0.0381, Z=3.79, $p<0.001$). A significant interaction between food source and wind speed (β=-00278, z=-2.25, $p<0.001$, figure 5) revealed that the number of groups increased as wind speed increased particularly for aspen-fed colonies; this trend seemed to be absent for maple-fed colonies. No other predictor variables were found to be significant.

3.3.2. Locomotion

Maple-reared caterpillar colonies were more likely to be observed walking than aspen-reared colonies (β=0.384, Z=2.32, p=0.02). No other predictor variables were found to be significant.

3.2.3. Performance

Fourth instar aspen-reared caterpillars were larger than fourth instar maple-reared caterpillars ($F_{[1,71]}$=185, p<0.001, figure 6).

Because two cases of caterpillar colony merging were experienced with caterpillars feeding on maple, survivorship was converted to a percentage of survival, combining the initial and final counts for the merged colonies. The t-test revealed that caterpillars feeding on aspen experienced a higher survivorship than those feeding on maple (t=3.33, p=0.0017, df=50, figure 7).

3.3.4. Measurements of natural movement

When examining the measured distance between the colony and its closest abandoned bivouac, no difference in this travelled distance between aspen-reared and maple-reared colonies was found ($F_{[1,77]}$=0.023, p=0.881, data not shown).

In regards to the distance between the colony and its egg mass, maple-reared colonies travelled significantly farther that aspen-reared colonies ($F_{[1,79]}$=4.46, p=0.038, figure 8). The date on which the measurements were taken were also found to be significant ($F_{[2,79]}$=4.93, p=0.010, figure 8). A post-hoc Tukey HSD test revealed that caterpillars at four days post-hatch travelled shorter distances than caterpillar at nine days post-hatch (p=0.045, figure 8) and

caterpillars at fourteen days post-hatch ($p=0.016$, figure 8). Caterpillars at nine and fourteen days post-hatch travelled similar distances from their respective egg masses ($p=0.79$, figure 8). No interaction between day post hatch and tree species was present ($F_{[2,79]}=1.35$, $p=0.264$, figure 8).

4. Discussion

4.1. Caterpillar performance and preference

In both laboratory and field experiments, high mortality of caterpillars feeding on maple was observed, especially in the former. Egg masses were collected from the Kenora and Dryden districts of Ontario from aspen trees, along the edge of the natural distribution of sugar maple (figure 1; Little, 1971), indicating that it is likely that the parental generation of forest tent caterpillars never came into contact with maple. Studies indicate that maple is, however, a viable food source for caterpillars (Lorenzetti et al., 1999). A previous study (Parry and Goyer, 2004) reared caterpillars using host plant species that differ from those that grow in their place of origin, rearing caterpillars originating from Manitoba, Canada; Michigan, USA; and Louisiana, USA, with leaves from aspen and maple trees from Manitoba, Canada. The researchers found that although caterpillars were smaller and took longer to develop when feeding on leaves from allopatric tree species when compared to local tree species, the caterpillars did survive and reach pupation.

Although high mortality for caterpillars feeding on maple was observed throughout the laboratory and field experiments, the main focus of the presented research was to compare the differences of foraging behaviors between caterpillars feeding on a higher and lower quality food source, where maple represent a lower quality food source when compared to aspen (Lorenzetti, 1993; Panzuto et al., 2001). Results for caterpillar performance, where caterpillars feeding on maple were smaller than those feeding on aspen, and food preference, where caterpillars feeding on maple took more numerous but smaller meals, were comparable to previous findings (performance: Lorenzetti 1993; Parry and Goyer, 2004; preference: Levesque et al., 2002; Etilé,

2008), indicating that maple indeed represents a lower quality food source when compared to aspen.

4.2. Effects of food quality on group size and splitting

In the presented experiments, forest tent caterpillar colonies feeding from maple increased locomotion, traveled farther, and split into smaller, more numerous groups. Maple-fed colonies were observed travelling farther that aspen-fed colonies, particularly at later developmental stages, which was to be expected as late instar caterpillars are generally more active (Fitzgerald 1995).

Remaining in larger groups benefits forest tent caterpillars by means of collective defense strategies (McClure and Despland, 2011), and group basking for thermoregulation (McClure, Cannell, and Despland, 2011). A past study (McClure and Despland, 2011) indicates that with increasing caterpillar group size, individual predation risk decreased regardless of predator. Furthermore, individuals at the center of the group were less likely to be attacked than those around the periphery of the group, an example of selfish herd effects (McClure and Despland, 2011). At later developmental stages, forest tent caterpillars are capable of defending themselves well enough that the costs of group living are no longer justified; at early instars, caterpillars experience the largest window of vulnerability, therefore, remaining in a larger group while young greatly increases the probability of survival to adulthood (Costa and Pierce, 1997). Colonies feeding on a lower quality food source in the presented experiments were more likely to separate into smaller, more numerous groups. When groups are more numerous and smaller, the probability of being attacked increases for all members as selfish herd effects are decreased (Hamilton, 1971), therefore caterpillar colonies feeding on a lower quality food source are

potentially more exposed to predation, however, may increase their chance of encountering a better quality food source.

Early instar caterpillars feeding on a favorable food source have been demonstrated to keep movement to a minimum in order to decrease predator conspicuousness (McClure and Despland, 2010). Therefore, by increasing locomotion and travelling farther while feeding on a lower quality food source, caterpillars effectively increase their probability of encountering a predator. Additionally, when forest tent caterpillars are engaged in locomotion, they can be found travelling in columns, as opposed to feeding or quiescent colonies which remain in larger concentrated mounds (Fitzgerald, 1995). By increasing movement, thus increasing time travelling in columns, caterpillars no longer benefit from selfish herd effects and increase the individual probability of being attacked, though again, increase the probability of encountering a better quality food source.

Forest tent caterpillars benefit from group basking, where groups reach optimal temperatures more readily than lone individuals (McClure and Despland, 2010). General benefits of reaching optimal temperatures are increased locomotion, and food uptake/processing (Dubois et al., 2009), leading to an increased growth and development rate (Levesque et al. 2002). Because forest tent caterpillar colonies feeding on a less favorable food source were more likely to separate into smaller groups, individuals would not reap the full benefits of group basking (McClure and Despland, 2010).

However, increasing movement and decreasing cohesion may potentially offset any possible negative effects. By remaining on a lower quality food source, caterpillars risk incurring opportunity costs as a minimal larval weight is required for pupation to occur (Etilé and Despland, 2008). Therefore, by initiating exploration and movement by leaving the colony,

smaller groups may reach a different, potentially higher quality food source. In the wild, a single tree presents a single host species, though leaf quality does change depending on sun or shade exposure (Panzuto et al., 2001), however, in densely packed forests, trees of different species do overlap where caterpillars may travel from one tree to another. In the field experiment, caterpillars were observed walking up maple and in one case, onto a different tree species (from sugar maple to *Fagus grandifolia*, American beech).

Therefore, it seems that food quality mediates decisions for forest tent caterpillars where separating into smaller, more numerous groups, effectively decreasing cohesion, benefits caterpillars as they may possibly encounter a higher quality food source, though risk predation. Indeed, forest tent caterpillar colonies have demonstrated conservative foraging strategies (McClure and Despland, 2011; Santana et al., 2015); however, after being nutrient deprived for an extended period of time, specifically protein-deprived, caterpillars initiate exploration (Colasurdo et al., 2007; McClure et al., 2013). As suggested in previous research, but not fully studied (Elgar, 1989 and references therein; see also Elgar, 1986), food quality can be a predictor of group size, demonstrated by the presented experiments (using a social insect, in this case the forest tent caterpillar, as a model species: see Nonacs and Dill, 1990).

4.3. Other variables affecting group size and splitting

Other ecological factors were found to mediate group decisions in terms of remaining cohesive or splitting into smaller groups, namely developmental stage (instar), colony size, and wind speed.

4.3.1. Developmental stage

At later developmental stages, forest tent caterpillars are generally more active, exhibit higher levels of independence, and lower levels of trail adherence, which has been linked to increases in food competition (Fitzgerald 1995; Despland and Le Huu, 2007), a reduced need for thermoregulation (McClure, Cannell, and Despland, 2011), and an increased ability in individual predator defenses (McClure and Despland, 2011); a common trend among other social caterpillar species (Costa, 2006). This suggests that caterpillars are faced with different ecological factors at different developmental stages, which has also been documented in various mammals and birds (Elgar, 1989). Fourth instar aspen-fed caterpillar colonies used in the presented experiments followed this trend, where the level of cohesion was at its lowest and independence at its highest. This, however, was not the case for second instar maple-fed caterpillars which spent less time in locomotion than first instar caterpillars, likely due to becoming feeble on the protein poor host, although they still engaged more in locomotion than first and second instar aspen-fed colonies (Panzuto et al., 20011 Lorenzetti, 1993).

4.3.2. Colony size

Regardless of host plant quality, larger colonies were more likely to split into smaller groups. A similar trend has been documented in mammals and birds (Elgar, 1989). This follows the trend of optimal grouping models where benefits increase as group size increases to a maximum, but then decrease afterward, demonstrating a peak fitness, though this peak can shift (Giraldeau and Caraco, 2000). In terms of the forest tent caterpillar, colony fragmentation may be due to three possible reasons (i) resource competition (ii) higher number of active individuals (iii) caterpillars exceeded optimal thermoregulatory temperatures.

i. It has been suggested that one main disadvantage of group living in general is resource competition, where individuals in larger groups are more likely to become nutrient deprived due to a lack of sufficient nutrition for the entire aggregation. Therefore, in cases of resource competition, it is beneficial for larger colonies to split into smaller groups as observed with the caterpillar colonies in the presented experiments. Similar findings have been documented with other social Lepidopteran caterpillars (Costa and Pierce, 1997), carnivores (Gittleman, 1989), birds, and mammals (Elgar, 1989).

ii. In a forest tent caterpillar colony, individual behaviors vary where individuals can be broadly classified into one of two behavioral categories; active or sluggish. Active individuals are more likely to initiate exploration without the presence of a pheromone trail, whereas inactive, or sluggish, individuals only move in the presence of a pheromone trail. If a certain percentage of any given colony is likely to be classified as active, then larger groups are more likely to have a higher number of active individuals (Nemiroff and Despland, 2007). Since active individuals are more likely to initiate exploration, these active caterpillars are responsible for leading the less active individuals into unmarked territory, essentially splitting the larger colony into smaller, more numerous groups.

iii. Forest tent caterpillars benefit from group basking (McClure and Despland, 2010), however overheating can occur, which can be detrimental to individual fitness. To avoid overheating, it is sometimes beneficial for larger colonies to separate into smaller groups, such as the case for the social Lepidopteran, *Eriogaster lanestris* (Ruf and Fielder, 2002). Therefore, it is possible that larger forest tent caterpillar colonies separate into smaller groups to avoid overheating.

4.3.3. Wind speed

As wind speeds increased, aspen colonies in particular were observed in smaller, more numerous groups. It is possible that increasing wind speeds stimulated the tactile setae of the caterpillars (Fitzgerald and Costa, 1986), mimicking the attack of an aerial predator or parasitoid, such as a wasp, where caterpillars naturally become more active, flick their heads, and bite in retaliation. Successful parasitoid attacks have been demonstrated to increase with increasing group size, therefore in cases of parasitoid attacks, it is beneficial for caterpillars to splinter into smaller groups (McClure and Despland, 2011). The disbanding due to higher wind speeds was more prevalent for caterpillar colonies feeding on aspen as they generally remained in one larger cohesive group, when compared to those feeding on maple, which were generally observed in more numerous groups. This suggests that there is a minimal group size required in order to maintain some benefits of group living (Despland and Le Huu, 2007). In general, solitary folivores have lower survival rates than group living species, therefore there remains some benefit in remaining in a group, regardless of the small size (Costa 2006; see optimal group size: Giraldeau and Caraco, 2000).

Alternatively, disbanding on aspen may be due to the physical characteristics of the leaf. Maple leaves have cylindrical petioles, unlike the flat petiole of an aspen leaf. The flat petiole gives the aspen its characteristic trembling movement in the wind, a type of movement not observed with maple leaves, which may have caused the caterpillars to disband at higher wind speeds (Petrides, 1986).

4.4. General conclusions

Though forest tent caterpillars do perform better on aspen, aspen abundance within a forest has been found to be negatively correlated to outbreak duration. The best predictor of duration was found to be forest fragmentation, with a positive correlation between forest edge and outbreak duration. In theory, fragmented forests may potentially limit the dispersion of forest tent caterpillar predators and parasitoids; this would in turn allow outbreaks within these areas to remain stable and last longer. A similar concept can be used to describe the negative correlation to aspen abundance and outbreak duration where small stands of aspen trees within a forest dominated by non-preferred hosts can isolate the caterpillar populations from predators, effectively increasing the duration of an outbreak (Roland, 1993). Furthermore, it is believed that forest tent caterpillar population cycling is due to delayed density-dependent parasitism (Cooke and Lorenzetti, 2006). As the presented experiments demonstrate that caterpillars feeding on a lower quality food source may potentially encounter higher rates of predation (or parasitism), these differences in behavior can contribute to an outbreak as predation and parasitism rates seem to be more of a contributing factor to the rise and decline of a population than the abundance of a preferred host tree species.

Splintering of maple-fed colonies may indicate either a negative consequence of the increased mobility due to protein deprivation, demonstrating a non-adaptive behavior, or that optimal group size is indeed different when feeding on a lower quality host compared to that of a higher quality, demonstrating an adaptive behavior. For example, smaller group sizes in the presence of low food density can be adaptive as smaller groups are more likely to find an adequate amount of food than larger groups (ex. mammals and birds: Elgar 1989 and references therein; Beauchamp, 2009 and references therein). Conversely, in the case of the American bison

(*Bison bison*), large groups form in open territory, but when introduced into a forested territory (considered unnatural for these bison), grouping breaks down as they can no longer maintain contact despite being more susceptible to predation in smaller groups regardless of territory, suggesting that the change in herd size is non-adaptive (Fortin et al. 2009).

Though maple can be considered a lower quality host for the caterpillars (Lorenzetti, 1993; Panzuto et al., 2001), past experiments have found that caterpillars feeding on different sections of the same maple tree perform differently (Fortin and Maufette, 2002), and the position of the maple tree, either at the edge of the forest or the interior of a forest, plays a key role in the nutritional quality of the foliage (Fortin and Maufette, 2000). One study (Fortin and Maufette, 2000) demonstrated that maple leaves on trees at the edge of a forest were higher in nitrogen, had higher levels of soluble sugars, and higher water content than trees at the interior, likely due to more sunlight exposure; pupal weight, survivorship, and egg production were all higher for caterpillars feeding on these edge leaves. Another study (Fortin and Maufette, 2002) indicated that vertical movement, toward higher leaves on a maple tree, may be beneficial for forest tent caterpillars. Leaves higher on a maple tree receive more sunlight, thus allowing for more nitrogen and soluble sugars, leading to higher pupal weight and survivorship for the caterpillars feeding on the foliage in the higher tree layers. In the case of different leaf composition in different layers of the tree, it would be beneficial for caterpillar colonies on lower layers of the tree to increase movement to higher layers (Fortin and Maufette, 2002), and group splintering might increase the probability that part of the colony reaches higher quality leaves. It is important to note, however, though caterpillars feeding on maple travelled farther and engaged more in locomotion in the presented experiments, maple foliage used for laboratory caterpillar rearing were selected from trees closer to the edge of the forest (in the case for Bois-De-Liesse),

and from single standing trees (from Complex Environmental St. Michel), similarly to the selected aspen trees. Additionally, maple trees used in the field experiment (from the Morgan Arboretum) received similar amounts of sunlight as aspen trees, and in this case, sunlight exposure was not found to be a statistically significant predictor variable for activity or cohesion.

Optimal group size for forest tent caterpillars have not been widely studied, though it has been demonstrated that in general, larger groups tend to have better survivorship due to increased thermoregulation and increased predator defenses. (Costa, 2006; McClure, Cannell, Despland., 2011; McClure and Despland, 2011; Santana et al., 2015). The same trend can be observed for *Euselasia chrysippe* (Lepidoptera, Riodinidae) (Allen, 2010), and the pine processionary moth (Pimental et al., 2012) where both social caterpillar species displayed higher larval survivorship in larger groups. The benefits of larger groups is further suggested by a study conducted with the eastern tent caterpillar (Costa and Ross, 2003), where colony merging, thus increasing group size and intracolony genetic variation, can increase task efficiency and parasite resistance, leading to higher survivorship. However, splintering into smaller groups may be beneficial when feeding on a poor quality host. Caterpillars increase movement and activity when protein-deprived (Colasurdo et al., 2007). It has been demonstrated that caterpillars can find a viable leaf on an artificial tree by initiating exploration, thereby increasing movement and travelling farther (Drouin, 2007). Therefore, splitting into more numerous groups may be adaptive in that the resulting larger network of pheromone trails suggest that a wandering group of caterpillars may potentially rejoin another group which has encountered either a higher quality, sun exposed leaf of the same tree (Fortin and Maufette, 2002) or a bridge to a different tree species, though this entails a cost of increased predation and decreased thermoregulation (McClure and Despland, 2010). Although past experiments with caterpillars feeding on maple have been largely

conducted in a laboratory setting, demonstrating higher survivorship with caterpillars feeding form a higher quality host (Parry and Goyer, 2004; Fortin and Maufette, 2000; Fortin and Maufette, 2002), it is possible that the increased mortality on maple in the field experiment was also due to increased predation rates. However, aspen trees contain extrafloral nectaries (Weber, 2015 and references therein), which have been demonstrated to attract parasitoid wasps (Patt et al., 1997), a predator of the forest tent caterpillar (Fitzgerald, 1995); maple trees do not contain such nectaries (Weber, 2015 and references therein). It remains to be seen if this plays an important role in forest tent caterpillar predation and if predators on maple and aspen differ. The presented experiments demonstrate that differences in foraging behavior of the forest tent caterpillar on the two food sources exist, therefore future research should focus on determining if predation rates differ on the food sources, which may provide insight into any other possible benefits or disadvantages of remaining cohesive or splitting up.

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Figures

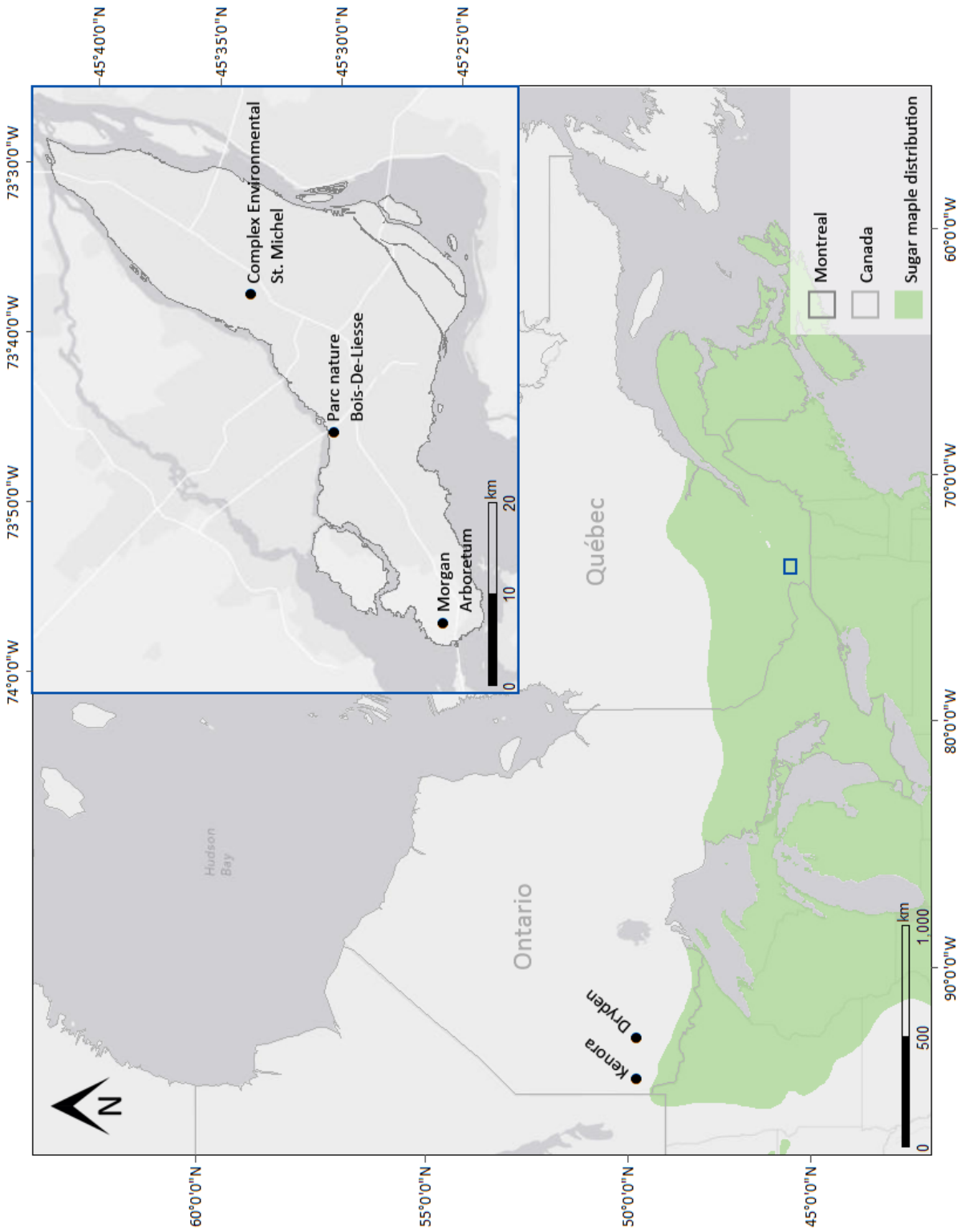

Figure 1. Map of locations used during experiments including: egg mass origin, host tree species origin, field study location, and sugar maple distribution.

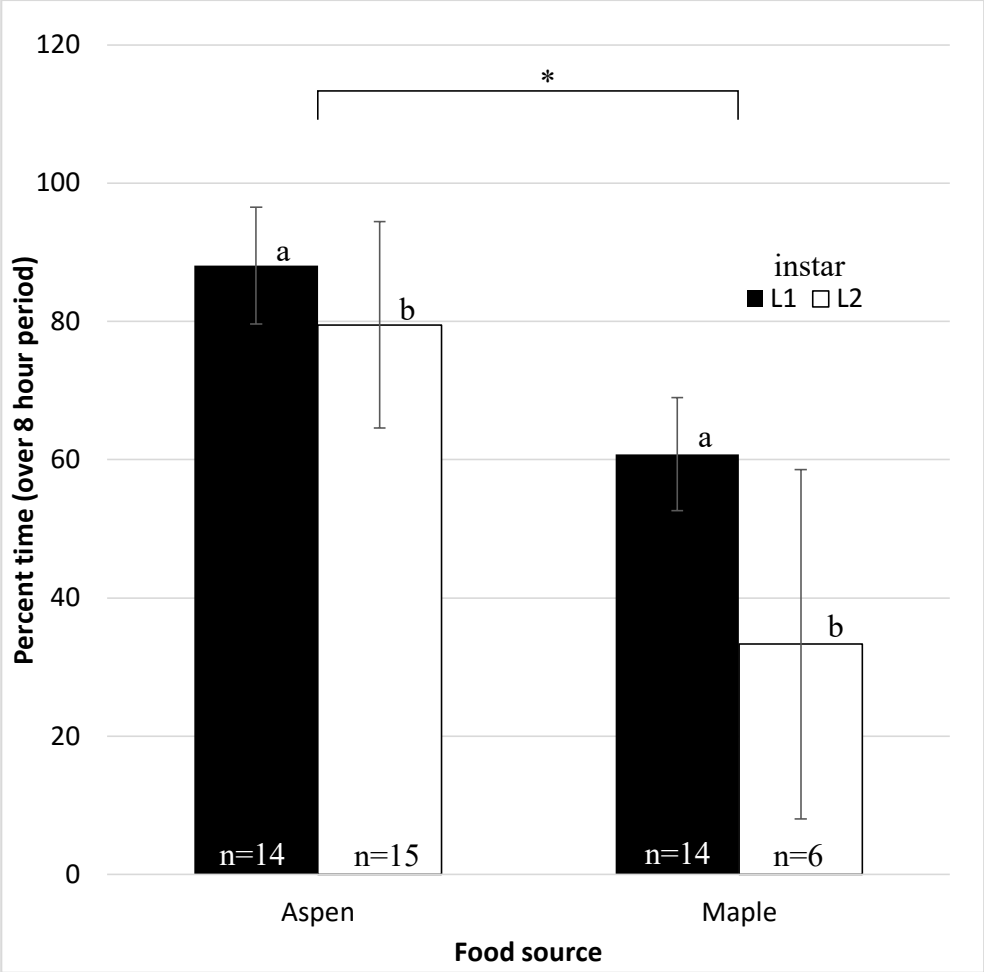

Figure 2. Percent time spent in one group (mean±95% CI). Asterisk (*) denotes significant differences between food source; different letters indicate significant differences between instar.

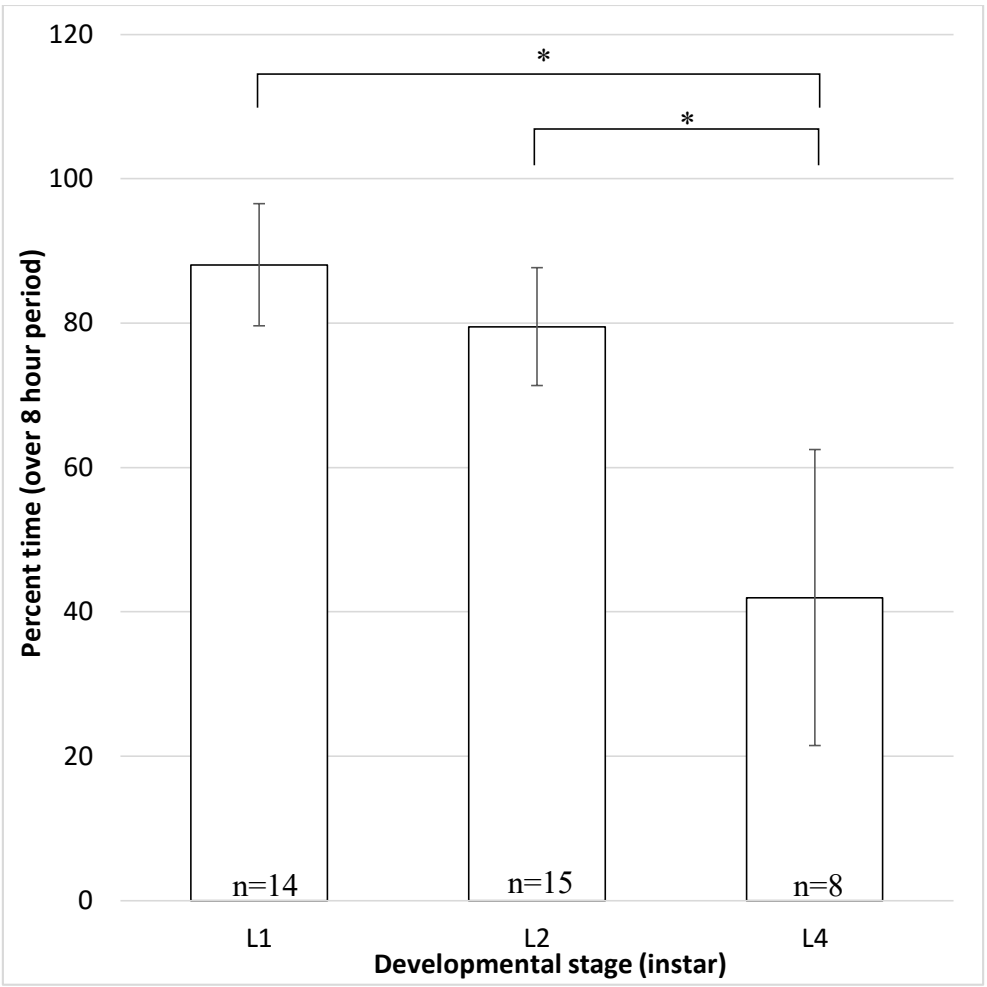

Figure 3. Percent time spent in one group (mean±95% CI) for aspen colonies only. Asterisks (*) indicate significant differences between instars.

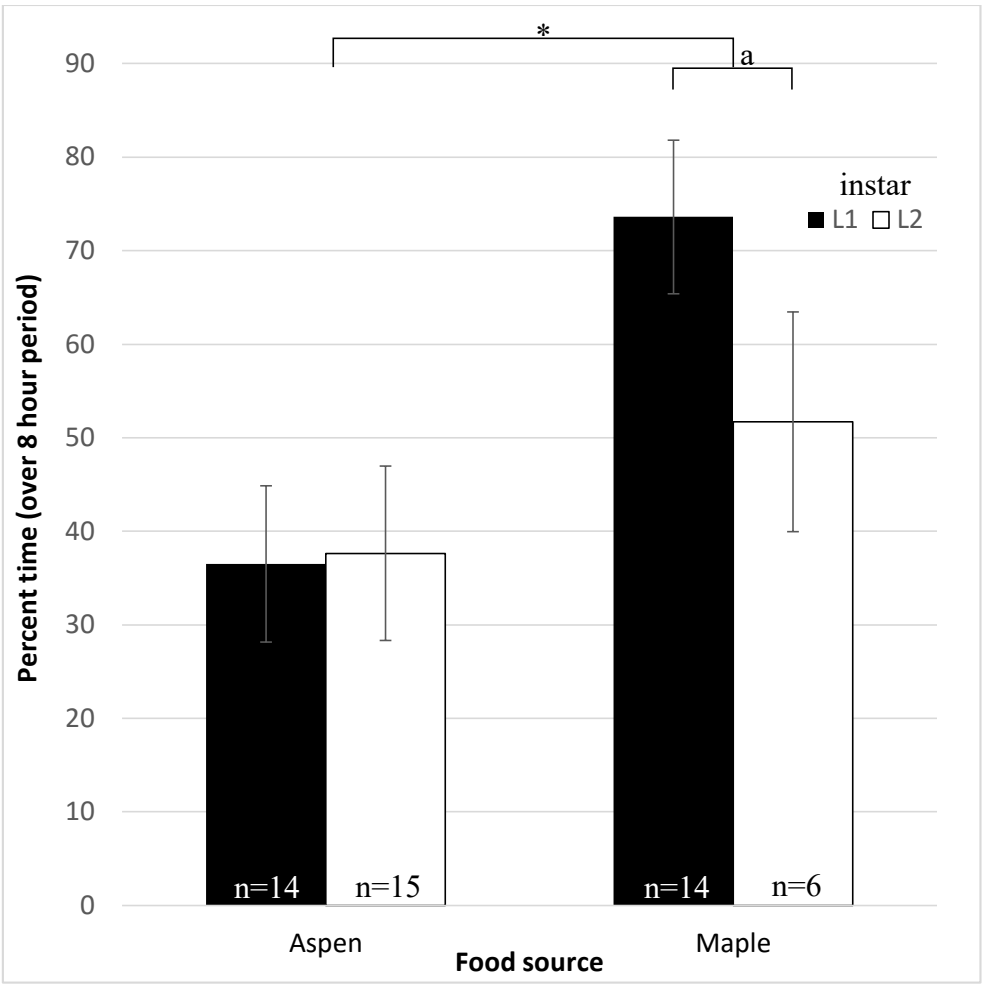

Figure 4. Percent time spent in locomotion (mean±95% CI). Asterisk (*) indicates significant differences between food source. Letter 'a' indicates significant differences between instars of maple-fed caterpillars.

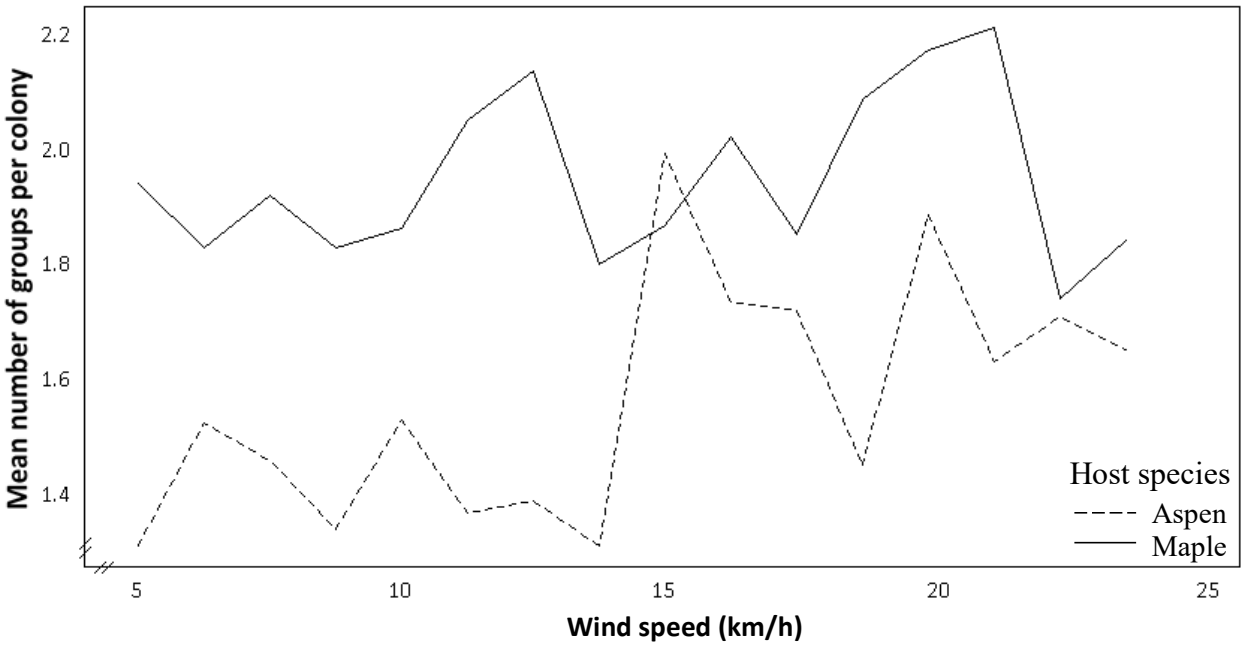

Figure 5. Interaction graph of wind speed (km/h) and mean number of observed caterpillar groups.

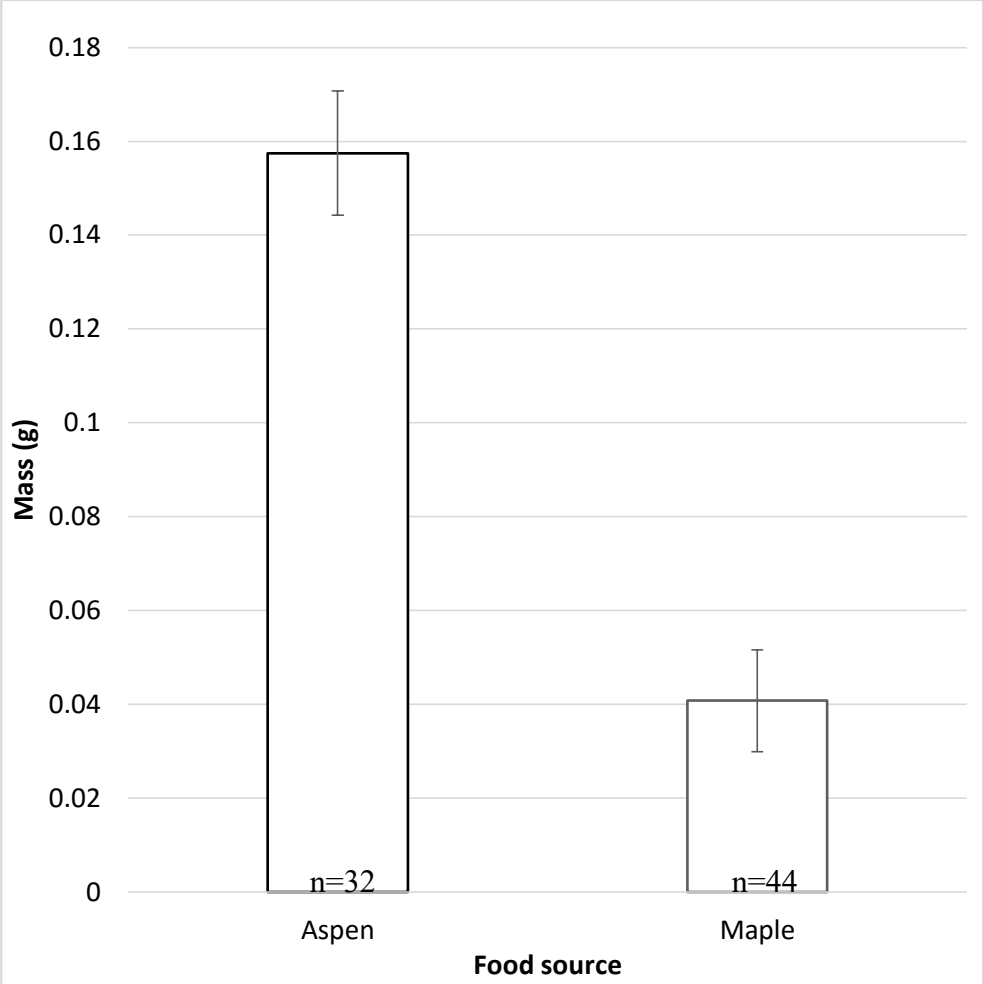

Figure 6. Mass (g) of fourth instar caterpillars (mean±95% CI).

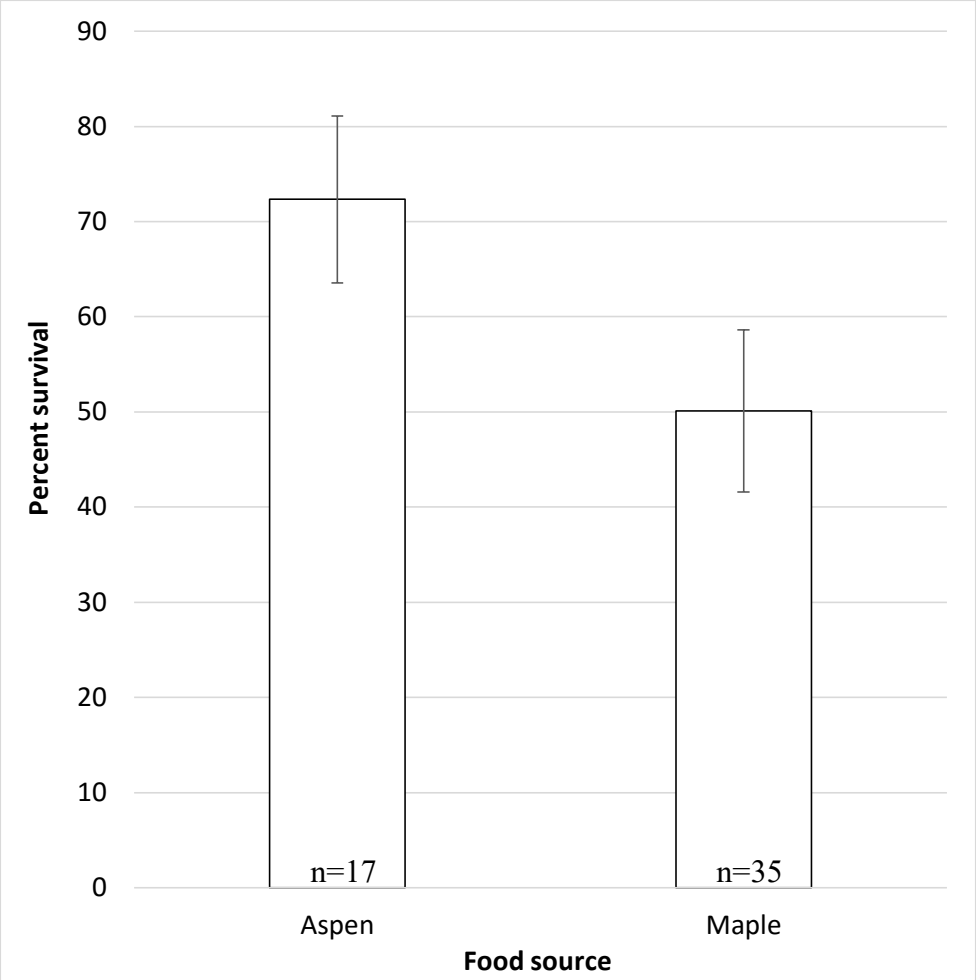

Figure 7. Percent survival of caterpillars (mean±95% CI).

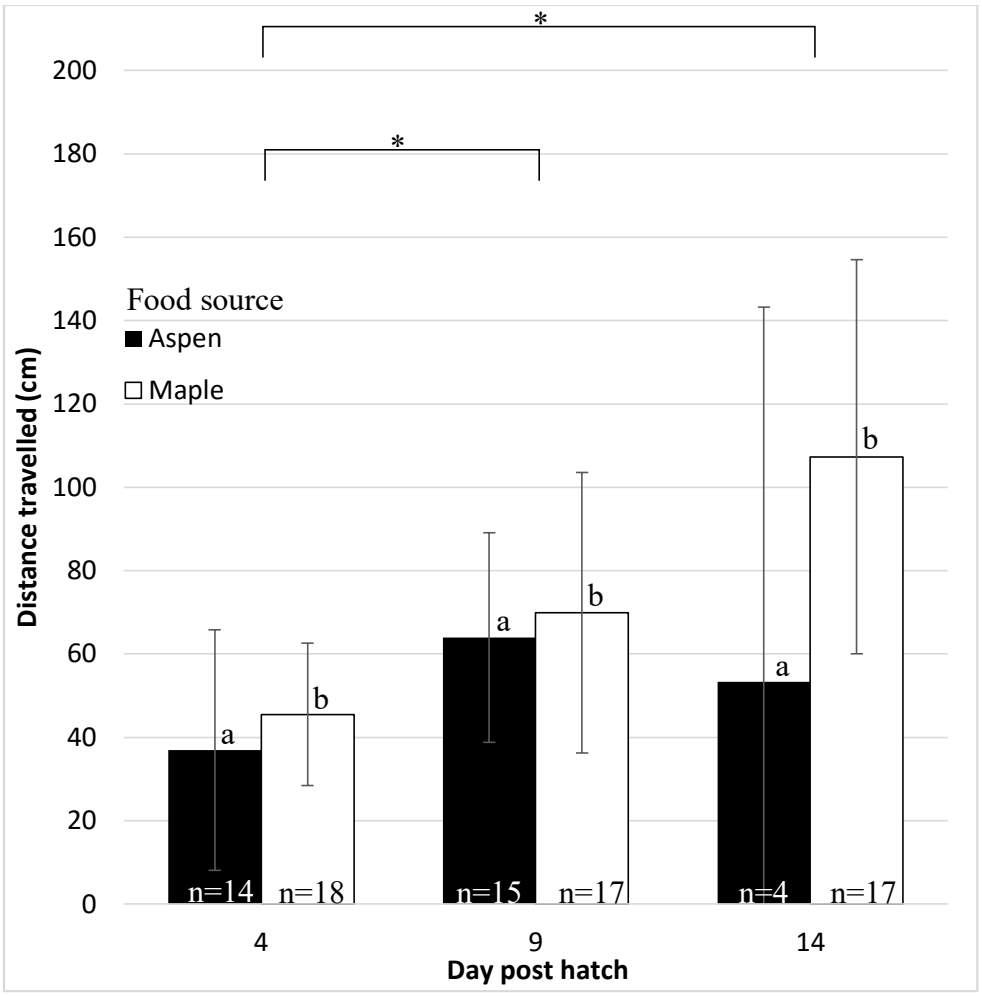

Figure 8. Distance between egg mass and colony (mean±95% CI). Asterisks (*) indicate significant differences between days; different letters indicate significant differences between host species.

Table 1. Summary of colony survivorship from laboratory experiment

	Food source			
	Aspen		Maple	
Developmental stage	# Regular Colonies	# Orphan colonies	# Regular colonies	# Orphan colonies
Egg Masses	20	-	28	-
L1	17	5	21	5
L2	16	5	9	1
L3	12	4	0	0
L4	7	2	0	0
L5	1	0	0	0